Acta Zootaxonomica Sinica, 32 (1): 21–34 (Jan., 2007) ISSN 1000-0739
动物分类学报

A SURVEY OF THE HOLARCTIC LINYPHIIDAE (ARANEAE), A REVIEW OF THE ERIGONINE GENUS *ZORNELLA* JACKSON, 1932

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Abstract The Holarctic erigonid genus *Zornella* has been surveyed. Four species are recognized in this genus, two Palaearctic: *Z. cultrigera* (L. Koch, 11879) & *Z. orientalis* sp. nov., and two Nearctic: *Z. armata* (Banks, 1906) & *Z. cryptodon* Chamberlin, 1920. It is demonstrated that neither nearctic species is conspecific with *Z. cultrigera* as was thought by Holm and other authors. *Z. orientalis* sp. nov. is described from northeastern Siberia. All of the species are illustrated and their distributions mapped.

Key words Spiders, Araneae, Erigoninae, Holarctic, *Zornella*, new species, redescription.

1 Introduction

Zornella is a small, peculiar, Holarctic genus of erigonine spiders with a convoluted nomenclatural history. Jackson (1932) created *Zornella* to accommodate a new species, *Z. mathiseni*, from Lapland. He recognized *Linyphia cultrigera* L. Koch, 1879 as congeneric. He was unable to examine the type but decided, because of character differences in its description, that it was distinct from *mathiseni*. Crosby and Bishop (1933) recognized that *Tmeticus armatus* Banks, 1906, described from Manitoba, Canada, belonged in *Zornella*. They sent a specimen to Jackson who deemed it to be identical with his *mathiseni*. They consequently synonymised *armatus* with *mathiseni*, and both with *cultrigera* based on their interpretation of Koch's description. They also synonymised *Diplocephalus cryptodon* Chamberlin, 1920, from Utah, with *cultrigera*, rendering the genus monotypic. Holm (1944, 1973) examined the type of *cultrigera*. He confirmed Bishop and Crosby's supposition that *mathiseni* was conspecific with cultrigera, and determined that the differences noted by Jackson were due to errors in Koch's description. He also synonymised *Gongylidium recurvatus* Strand, 1901, from Norway, with *cultrigera*. No further taxonomic attention was paid to the genus until the conspecificity of certain Siberian populations was questioned by Logunov *et al*. (1998), Marusik *et al*. (2000) and Marusik (2005a-b), and Buckle *et al*. (2001) pointed out that *cryptodon* was wrongly synonymised with *cultrigera*. Aakra (2002), in a review of several hitherto unplacable species described by Embrik Strand, presented a strong, though not totally conclusive, argument that *Pseudogonatium fuscomarginatum* Strand 1901 was a synonym of *cultrigera*. This would make *Pseudogonatium* Strand, 1901 a senior synonym of *Zornella*. Fortunately, *Pseudogonatium* qualifies for automatic suppression under ICZN (1999) rules, so nomenclatural stability is maintained (Platnick, 2006).

The nomenclatural complexity was compounded by Roewer who, in his Katalog der Araneae, Vol. 1 (1942), idiosyncratically accepted Crosby and Bishop's synonymy of *armatus*, *mathiseni* and *cryptodon* while ignoring their synonymy of these taxa with *cultrigera*. In consequence, he listed two species: *armatus* (including *mathiseni* and *cryptodon*) with a Holarctic distribution, and *cultrigera*, confined to Siberia. This placement has been followed by the catalog's successors to the present day (e. g. Platnick, 2006), while authors dealing with *Zornella* have followed Crosby and Bishop, and Holm, in considering all of the names to be synonyms (e. g. Hackman, 1954; Palmgren, 1976; Belanger & Hutchinson, 1992; Eskov, 1994; Dondale *et al*., 1997; Paquin & Dupérré, 2003).

We have made a detailed review of members of the genus, in the course of which we established that *cultrigera* (with *recurvatus* and *mathiseni* as synonyms) occurs across northern Europe and Asia, that *armatus* and *cryptodon* are distinct Nearctic species, and we here describe a new species from northeastern Siberia.

2 Material and Methods

Material was examined from the American Museum of Natural History, New York (AMNH), Canadian National Collection, Ottawa (CNC), D. J. Buckle's personal collection, Saskatoon (DJB), Institute for the biological Problems of the North, Magadan (IBPN), R. G. Bennett's personal collection, Victoria (RGB), Strickland Museum, University of Alberta, Edmonton (UASM), and Zoological Museum, University of Turku (ZMUT), and Zoological Museum of the Moscow State University (ZMMU). Material from Kirill Eskov's collection, stored in ZMMU is marked as ZMMU-KE. The map is based on material studied during this project, our earlier identifications published in several papers and literature data.

Epigynes were cleared in a mixture of glycerol and

Received 21 Sep. 2006, accepted 31 Oct. 2006.

lactic acid, and palps were photographed while immersed in glycerol-lactic acid.

Names of countries are capitalized, the largest administrative units in each country are in bold-italic.

Illustrations were made using a transmitted light microscope with drawing devices. SEM photographs were made with SEM Jeol JSM-5200 in the Zoological Museum, University of Turku. Figures were made in different years, which is why drawing styles differ. All measurements are given in mm.

The following abbreviations have been used in illustrations: *Bi*- bifid tip of *Ft* or Ta; *Ci*- cheliceral ridge; *Cl*- cephalic lobe; *Cp*- cephalic pit; *G*- ridge in thoracic part of carapace; *Da*- dorsal tibial apophysis; *Eb*- basal part of embolus proper; *Em*- embolus proper; *Er*- epigynal rostrum; *Et*- ED tailpiece; *Fd*- denticle on *Ft*; *Ft*- frontal tooth; *Lp*- lateral plate; *Lt*- mastidion (= large tooth); *Mc*- concavity of maxillae; *Me*- embolic membrane; *Mp*- median plate; *Pa*- patellar tooth; *Pr*- protegulum; *Ps*- paracymbial setae on *Pt*; *Pt*- terminal part of paracymbium; *Ri*- ridges; *Se*- terminal part of epigynal sulci; *Sm*- serrated macrosetae; *Su*- sulci of carapace; *Ta*- retrolateral tibial apophysis; *Th*- hollow of *Ta*; *Tl*- lobe of tibia or trochanter; *Tm*- weakly sclerotised ridge of tibia; *Tr*- trichobothrium; *Tr*- trichobothrium; *Ts*- tegular sac; *Wr*- width ratio.

Zornella **Jackson, 1932**

Pseudogonatium Strand, 1901: 38. Older name suppressed for lack of use (see Platnick, 2006)

Zornella Jackson, 1932: 107, pl. 1, f. 1-4

Type species: *Z. mathiseni* Jackson, 1932 from Lapland. Bonnet (1959) and Platnick (2006) refer to *Linyphia altrigera* L. Koch, 1879 from Chantajskoj (= Khantayka) on the Yenisei River, as the type species, although Jackson (1932) clearly indicated *Z. mathiseni* as the generotype.

Etymology. According to Holm (1963) this genus was named after the prominent Swedish artist Anders Zorn (1860-1920) because of the resemblance of the serrated paracymbial setae to an artist's paint brush.

Description. Large sized erigonines (3.0-4.6 mm). Carapace color varies from orange to red and abdomen color from dark gray to black in fully pigmented specimens of all species. The carapace is low and flattened. The male carapace modified in all species: the carapace slightly raised behind the ocular area, forming a cephalic lobe (*Cl*); small sulci (*Su*) or cephalic pits (*Cp*) present (Fig. 1). There is no significant interspecific variation of the cephalic modifications. Tibia with 2-2-1-1 dorsal spines; macrosetae slightly longer than tibia diameter, but very weak. Metatarsus I with dorso-basal macroseta well developed in *Z. orientalis* sp. nov. Tm I ranges from 0.63 to 0.81. Tm IV present. Male chelicera modified: with a large, downward-pointing frontal tooth (*Ft*), the shape of which is species specific (Figs. 7-10). All species also have a large seta-tipped mastidion (or large tooth, *Lt*) just above the promarginal row of teeth. In *Z. armata* the mastidion is usually distinctly bifid, in other species this subdivision less distinct. Inner side of chelicera has a distinct ridge or carina (*Ci*) just behind the retromarginal tooth row (Fig. 9). Maxillae modified (Figs. 3-4); they are wide and project sidewise, and their frontal margin is strongly concave (*Mc*). *Zornella altrigera* is known to have branched trachea extending into the cephalothorax (Millidge 1984). *Zornella* has inverted size dimorphism, with the male larger than female, except in *Z. cryptodon* where the sexes are equal in size.

Copulatory Organs

Male palp. Male palp of moderate length. Trochanter with two ventral lobes (*Tl*) (Fig. 3). Patella with two more or less distinct apical apophyses beneath (*Pa*) (Fig. 28). Tibia swollen and with a cup-shaped hollow apically. Cymbium attached to mesal margin of cup, and three marginal apophyses present. There are two apophyses on dorsal side (*Da*, *Ta*) and a well developed ventro-retrolateral lobe (*Tl*) (Figs. 27-28). Dorso-retrolateral apophysis (*Ta*) reduced in *Z. cryptodon*. Inner-retrolateral side of tibial cup with longitudinal ridges (*Ri*) associated with the base of retrolateral tibial apophysis easily visible, especially in *Z. cryptodon* (Fig. 19). Dorsal tibial apophysis (*Da*) with a rounded tip slightly bent in direction of retrolateral apophysis. The two apophyses are connected by a weakly sclerotised ridge (*Tm*). Tibia normally with three trichobothria (*Tr*), though occasionally there is an extra one in either the ectal or mesal row. Millidge (1977) was in error when he reported 5 trichobothria for this genus. Tibia with several slit organs. This character has been reported from only a few genera, but has probably been frequently overlooked. Paracymbium small, with a curved, bilobed, heavily sclerotized distal arm (*Pt*) which bears several small setae. The basal arm is unsclerotized and appressed to surface of cymbium. Three long, serrated macrosetae (*Sm*) arise from near its tip (Fig. 28). Embolic division with a long, thin embolus having an S-shaped loop (*Em*), a straight, parallel sided, truncately tipped embolic membrane (*Me*), and a short, ovate tailpiece (Fig. 5). Suprategular apophysis as shown in Fig. 6.

Epigyne. Epigyne without fovea; median plate bordered on both sides by deep invaginations (or sulci). Central part of median plate extended into more or less distinct lobe (= epigynal rostrum, *Er*, Figs. 58, 61). This lobe is poorly developed or nearly absent in most of specimens of *Z. armata*.

Species Specific Characters

All species of *Zornella* are very similar and there are only few characters that allow their separation. Most of these characters are in the shape of copulatory organs and only a few involve somatic characters. Below we survey all species-diagnostic features.

Male carapace. The thoracic part of the carapace of *Z. armata* has a distinct submarginal ridge (Cr). This character is present, though less developed, in *Z. ultrigera*, where it is clearly visible only in SEM photos (Fig. 1).

Male chelicera. All species can be more or less easily diagnosed by the shape of the frontal tooth of the chelicera (*Ft.*, Fig. 2): its dorsal side can be shallowly sloped (*Z. cryptodon*), steeply sloped (*Z. cultrigera* and *Z. orientalis* sp. nov.) or can bear a denticle (*Z. armata*). It is identically shaped in *Z. cultrigera* and *Z. orientalis* sp. nov.

Position of trichobothrium. The Tm I ratio is lower in *Z. cryptodon* than in the other species.

Epigyne. As with the male chelicerae, all species, except for *Z. ultrigera* and *Z. orientalis* sp. nov., can be easily separated by the shape of the epigynal rostrum. These two sibling species can be separated, with some difficulty, by the shape of epigynal sulci and by the relative size of the rostrum.

Male palp. Shape of the bulbus is very similar in all species, but good diagnostic characters are found in the shape of palpal tibia, especially the shape and relative length of retrolateral tibial apophysis. There are some differences in the depth of the hollow of the paracymbium.

Relationships. The frontal tooth of the male's chelicera is an unique feature. It appears not to be homologous with the mastidion, a feature scattered throughout the Linyphiidae, as a typical mastidion is present on the chelicera as well. The apical ventral apophyses of the male's palpal patella are also unique. In other genera, (e. g. *Tmeticus* Menge, 1868; *Erigone* Audouin, 1826; *Hylyphantes* Simon, 1884) having apical ventral apophyses, they are single and midventral in position, while in *Zornella* they are paired and in pro-ventral and retro-ventral positions.

The serrated hairs on the basal arm of *Zornella*'s paracymbium are similar to those occurring in *Islandiana* and *Valdivialla* Millidge, 1985. Neither of these genera has other characters suggesting a relationship to *Zornella*, or each other.

Jackson (1932), in describing *Zornella*, suggested its close relationship to *Tmeticus*, because of the mastidion, the very small dorsal tibial spines, the spine-like embolus, the simple bulb, the well developed maxillae, and other characters. It is possible to add that both genera have a red carapace and dark abdomen. Jackson compared *Zornella* with *Oedothorax* Bertkau, 1883 as well, and concluded that *Zornella* occupied an intermediate position between *Tmeticus* and *Oedothorax*. Although *Tmeticus* resembles *Zornella* somewhat in colour and in the presence of a mastidion, it lacks sulci and a frontal cheliceral tooth, has unmodified maxillae, and different type of embolic division, with a much shorter embolus, and a strong anterior radical process, absent in *Zornella*. *Oedothorax* has no significant similarities with *Zornella*.

Millidge (1977) placed *Zornella* in his *Leptorhoptrum*/*Lophomma* genus group, which appears to be a heterogeneous assemblage of basal and distal erigonines (sensu Hormiga, 2000). Within this group, the one genus with any real resemblance to *Zornella* is *Tiso*, which has a similar embolic division. However, EDs with thin, looped emboli and short tailpieces are common among the distal erigonines. While *Zornella*'s closest relative is not obvious, it seems likely that the genus belongs somewhere within that large group of distal erigonines which Millidge placed within his *Pelecopsis* and *Savignia* groups, and which share with it a similar ED structure and cephalic pits.

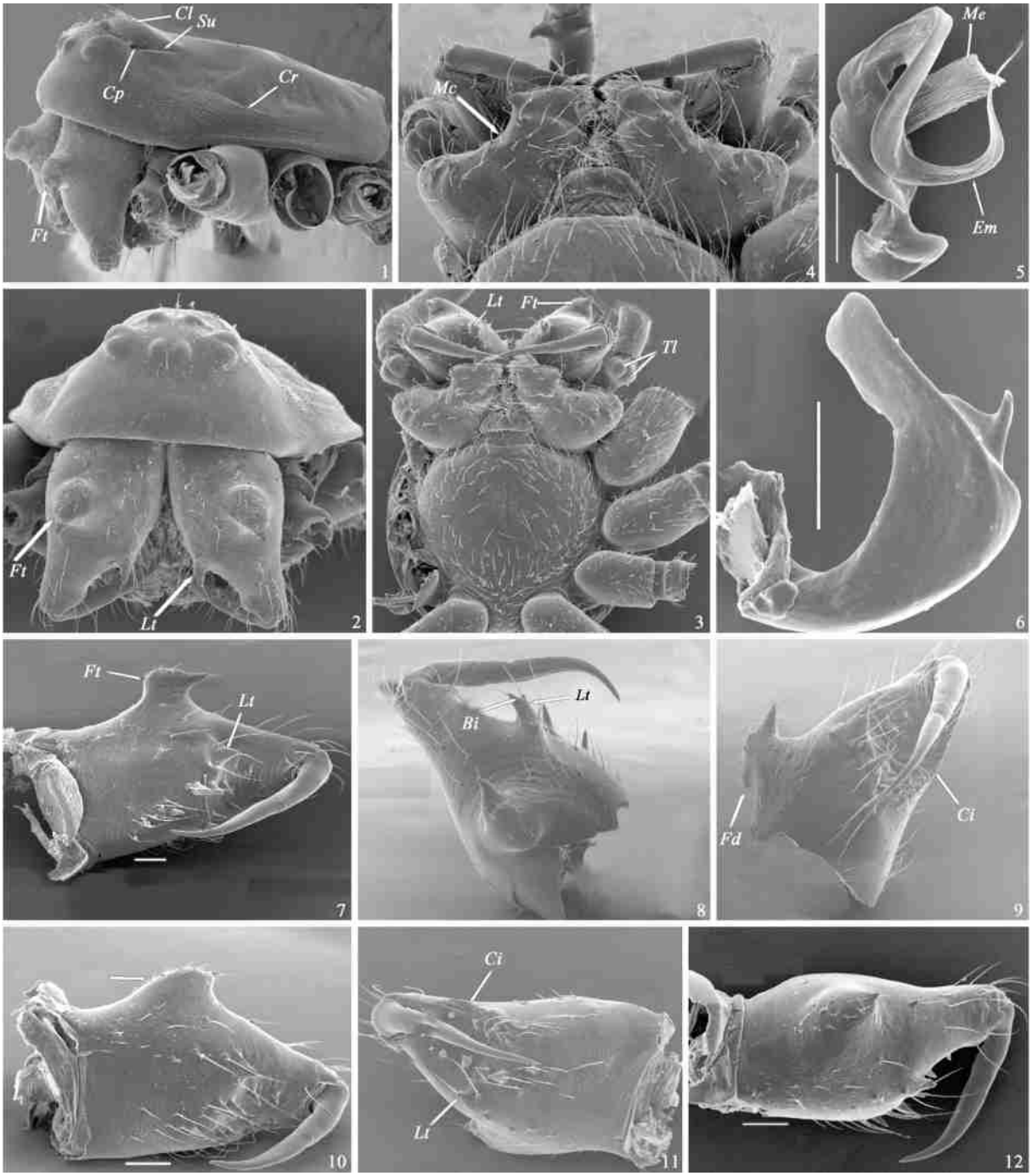
Composition and distribution. Four species of *Zornella* are treated here as a valid: *Z. armata* (northern Nearctic), *Z. cryptodon* (western Nearctic), *Z. ultrigera* (Europe to Yakutia), and *Z. orientalis* sp. nov. (northeast Siberia). This genus is found throughout the Holarctic except for western Europe south of Fennoscandia (Finland, Sweden and Norway). The southernmost boundary of this genus in Eurasia lies in East Kazakhstan and Mongolia at about 48° N latitude. The northernmost records are from northern Fennoscandia (70° 10′ N). Both boundaries are formed by *Z. ultrigera*. In the Nearctic the range of the genus has more southern limits: from 68° N to about 40° (Utah).

Survey of species

Zornella cultrigera **(L. Koch, 1879)** (Figs. 1-6, 13-18, 28, 34-36, 45-47, 55-57, 68-72)

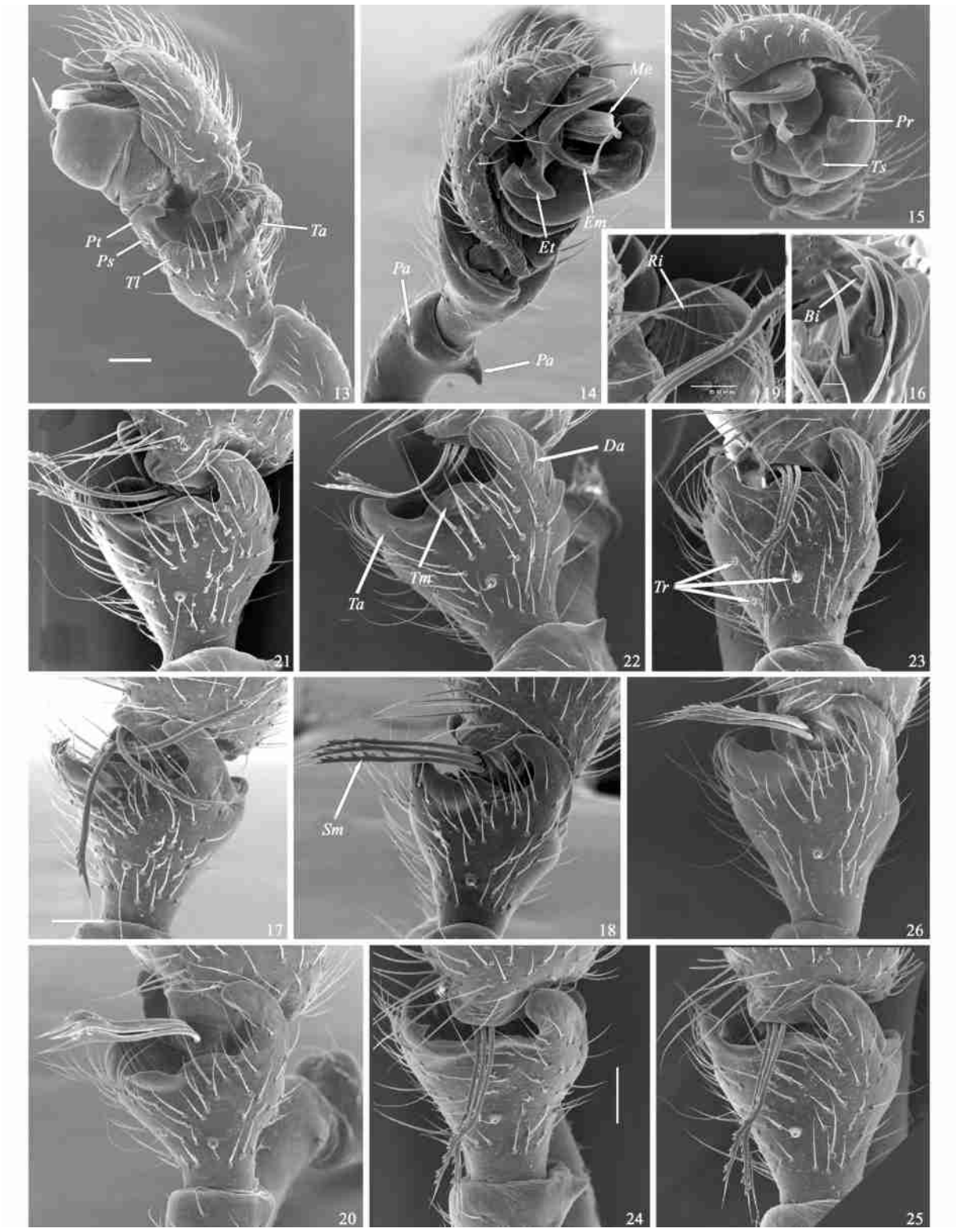
Linyphia c. L. Koch, 1879: 11, pl. 1, f. 2 (D ♂♀).
Gongylidium recurvum Strand, 1901: 33, f. 6 (D♀).
Pseudogonatium fuscomarginatum Strand, 1901: 38 (D♀).
Oedothorax recurvus: Strand, 1906: 445.
Stylothorax recurva: Reimoser, 1919: 73.
Pseudogonatium fuscomarginatum: Schenkel, 1931: 962, f. 6 (♀).
Z. mathiseni Jackson, 1932: 107, pl. 1, f. 1-4 (D ♂).
Z. c.: Holm, 1944: 127, f. 5a-c (♂♀).
Z. c.: Palmgren, 1976: 116, f. 5.9-12 (♂♀).
Z. c.: Millidge, 1977: 6, f. 5 (♂).
Z. sp. 1. (cf. cultrigera): Logunov *et al.*, 1998: 138.
Z. cf. *ultrigera*: Marusik *et al.*, 2000: 75.

Material examined. Norway: Finnmark 4♀♀ (ZMUT), Nesseby Mortensnes, bog (70° 10′ N), Summer, 1973 (S. Koponen). Finland (all in ZMUT): Varsinais-Suomi: 1 ♂, Paimio, Viksberg, 670: 25, 4 Nov. 1966 (P. T. Lehtinen). Etelä-Häme: 2 ♂♀ Somero, Koisthuhta, 674: 30, 22 Sep.



Figs 1-12. Morphology of the males of *Zorndla* species: *Z. altrigera* (1, 5-6. Mirnoye. 2-4. Chambe), *Z. orientalis* sp. nov. (7. Magadan), *Z. armata* (8-9. Alberta) and *Z. cryptodon* (10-12). 1-3. Cephalothorax, lateral, frontal and ventral, respectively. 4. Mouth parts, ventral. 5. Embolic division, prolateral. 6. Suprategular apophysis. 7, 9-11. Chelicera, mesal. 8, 12. Chelicera frontal. Scale bars= 0.1 mm. All chelicera are in equal scale. Abbreviations: *Bi*- bifid tip of *Ft*; *Ci*- cheliceral ridge; *Cl*- cephalic lobe; *Cp*- cephalic pit; *G*- ridge in thoracic part of carapace; *Em*- embolus proper; *Fd*- denticle on *Ft*; *Ft*- frontal tooth; *Lp*- lateral plate; *Lt*- mastidion; *Mc*- concavity of maxillae; *Me*- embolic membrane; *Su*- sulci of carapace; *Tl*- lobe of trochanter.

1974 (H. Hippa & R. Mannila). Satakunta: 12 ♂♀ Huittinen, Karhiniemi, 679: 25, 28 Aug. 1974 (R. Mannila). Pohjois-Häme: 1 ♂ Virrat, Ohtola, 691: 33, Ledum-Betula nana mire, 5 June 1977 (P. T. Lehtinen). Pohjois-Karjala: 2♀♀, Lieksa, Pielisjärvi, Märäsvaara, 703: 62, 15 June 1967 (P. T. Lehtinen); Koillismaa: 1♀ Kuusamo, Torankijärvi, 731: 60, 7 July 1967 (M. Saaristo). Kittilän Lappi: 2♀♀, Kolari, Sieppijärvi, 744: 37, 20 June 1967 (M. Saaristo). Enontekiän Lappi: 1 ♂, 3♀♀, Enontekiö, Kilpisjärvi, Saana, 767: 25, 27 July 1969 (A. Suormala). Inarin Lappi: 1 ♂, 3♀♀, Utsjoki, Kevo, 774: 50, mountain birch forest (150 m), 5 July-5 Sep. 1973 (S. Koponen); 1 ♂, 5♀♀, Utsjoki, Kevo,

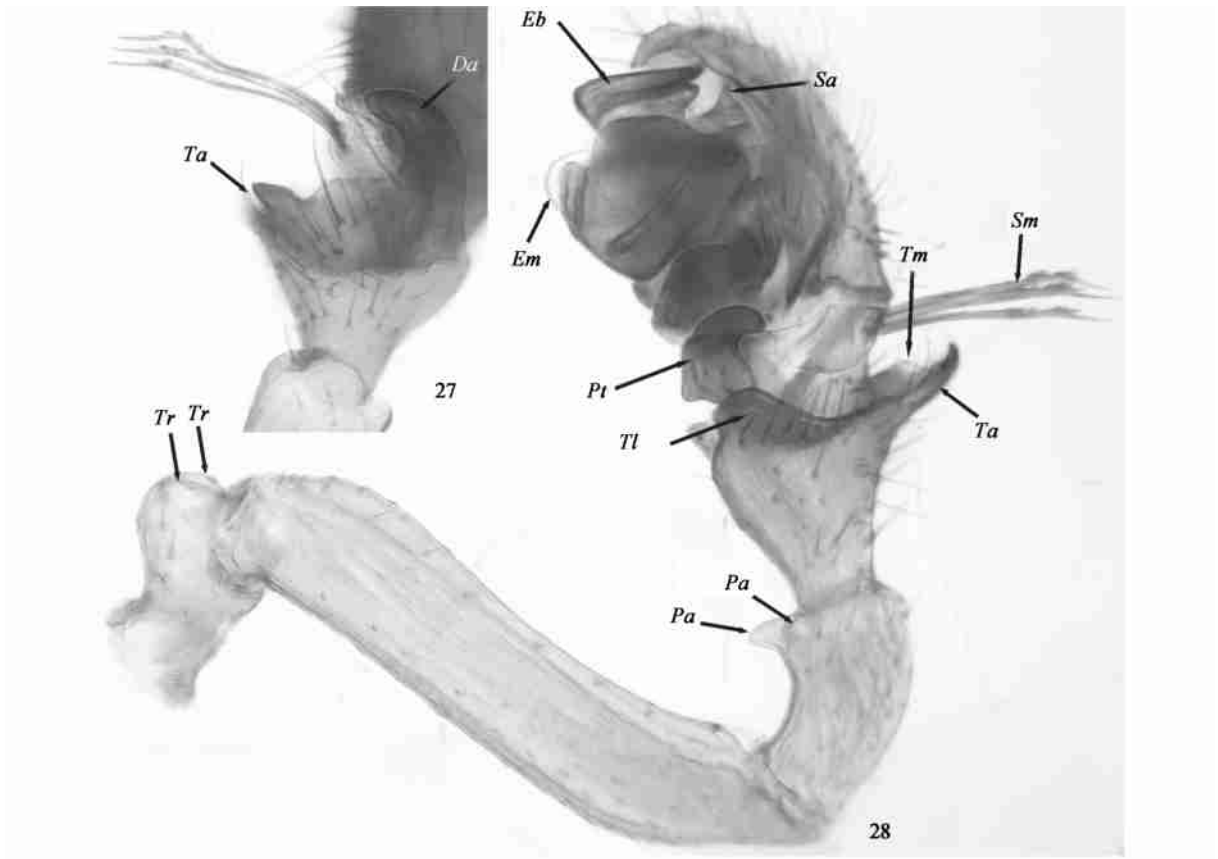


Figs 13-26. Male palp of *Zornella altirigera* (13-18. Mirnoye), *Z. cryptodon* (19-20), *Z. armata* (21-25. Alberta) and *Z. orientalis* sp. nov. (26. Magadan). 13-15. Retrolateral, prolateral and from above, respectively. 16, 19. Retrolateral tibial apophysis, from above. 17, 20-26. Palpal tibia, dorsal. 21-25. Different turns, showing angle sensitive shape of tibial apophysis and flexibility if serrated hairs. Scale bars= 0.1 mm. Abbreviations: *Bi*- bifid tip *Ta*; *Da*- dorsal tibial apophysis; *Emb*- embolus proper; *Et*- ED tailpiece; *Fd*- denticle on *Ft*; *Ft*- frontal tooth; *Lp*- lateral plate; *Lt*- mastidion; *Me*- embolic membrane; *Pa*- patellar tooth; *Pt*- protegulum; *Ps*- paracymbial setae on *Pt*; *Pt*- terminal part of paracymbium; *Ri*- ridges; *Sm*- serrated macrosetae; *Ta*- retrolateral tibial apophysis; *Tm*- membrane of tibia; *Tr*- trichobothrium; *Ts*- tegular sac.

Jesnalvaara, 774: 49, low alpine heath (320 m), 5 June-5 Sep. 1973 (S. Koponen). RUSSIA. Altai: 1♀

(ISEA), 32km SSW of Ust'-Koksa Vill., Petrushkina River upper reaches, 1 400-1 500 m, forest, 50°03′ N, 85°21-22′ E, 5-6 June 2005 (R. Dudko); 1♀ (ZMUT), SW Altai, 10 km S Katanda, 6 July 1983 (H. Hippa); 1♀ (ZMUT), SW Altai, Kuragan, Sphagnum, 24 July 1983 (H. Hippa). Tuva: 1 ♂, 1♀ (ZMUT), Tannu-Ola Mt. Range, S slope, 50°50′ N, 94°18′ E, 2 120 m, Pinus cembra-Larix forest, 8-17 June 1995 (S. Koponen); 1♀ (ISEA), East Tannu-Ola Mt. Range, 20 km NW of Khol'-Oozhu, Kangai-Kyry Mt., 50°50′ N, 94°19′ E, Larix-moss-stony forest-tundra, 2 175 m, 12 July 1989 (D. V. Logunov); 4♀♀ (IBPN), Sangelen Mt. Range, the upper reaches of Dzherr-Aryk (Ck), 50°28′ N, 95°24′ E, 2 030 m, mountain bush tundra, 16-18 July 1996 (Yu. M. Marusik); 10♀♀ (ZMUT), Tannu-Ola Mt. range, N slope, 50°38′ N, 95°18′ E, 1 300 m, Betula-Larix-Picea-Pinus cembra forest, 6-19 July 1995 (S. Koponen); 2♀♀ (IBPN), Sangelen Mt. Range, the middle reaches of Kargy River, 50°35′ N, 97°05′ E, 1 300 m, 2-4 July 1996 (Yu. M. Marusik); 4♀♀ (IBPN), Sangelen Mt. Range, the middle reaches of Kargy River, 50°31′ N, 97°03′ E, 1 400 m, 28-30 July 1996 (Yu. M. Marusik). Evenkiya: 19 ♂♀ (ZMMU-KEC), Taimura River, Chambe River mouth, meteorological station "Kerbo", floodplain willow stand, litter, 21 Aug. 1982 (K. Yu. Eskov). *Krasnoyarsk* Prov.: 1 ♂, 10♀♀ (ZMMU-KEC), Mirnoye, Varlamovka, mature taiga, 24 Sep. 1979 (K. Yu. Eskov); 24 ♂♀ (ZMMU-KEC), Mirnoye, Burovaya, mature taiga, 20-23 Aug. 1979 (K. Yu. Eskov); 1 ♂ (ZMMU) Mirnoye, 13 Aug. 1977 (?); 1 ♂ (ZMMU-KEC), West Sayan, Yermakovskoye Vill., carex bog in taiga, 21 Aug. 1984 (A. B. Ryvkin). Buryatia, 5♀♀ (ZMUT), Svyatoi Nos Peninsula, Monahovo, pine forest, 53°40′ N, 109°00′ E, 600 m (S. Koponen). *Chita* Area: 1♀ (ZMMU) Sokhondo Reserve, Verkhniy Bukukun, 21 July 1990 (S. N. Danilov). Yakutia: 1♀ (IBPN) South Yakutia, Maloye Toko Lake (Ca 56°N, 131°E), 25 July 1990 (N. N. Vinokurov). Kazakhstan: East-Kazakhstan Area: 3♀♀ (ZMMU), Zaisan City environs, Dzheminei River, Larch forest, 17 June 1989 (C. V. Ovchinnikov). Mongoilia: *Tov* (= Central) Aimak: 1 ♂, 11♀♀ (IBPN), Bayantsogt Somon, environs of Ulan-Bator, 48°07′ N, 106°54′ E, 1 700 m, 18 May 1997 (Yu. M. Marusik).

Description. Measurements (♂/♀, from Mirnoye). Total length 3.75-4.25/3.3-3.75. Carapace:



Figs 27-28. Male palp *Zomella cryptodon* (27) and *Z. altrigera* (28, Mirnoye). 27. Tibia, dorsal. 28. Whole palp, retrolateral view. Abbreviations: *Eb*- basal part of embolus proper; *Em*- embolus proper; *Er*- epigynal rostrum; *Pa*- patellar tooth; *Pt*- terminal part of paracymbium; *Sm*- serrated macrosetae; *Ta*- retrolateral tibial apophysis; *Tl*- lobe of tibia and trochanter; *Tr*- lobe of trochanter; *Tm*- membrane of tibia.

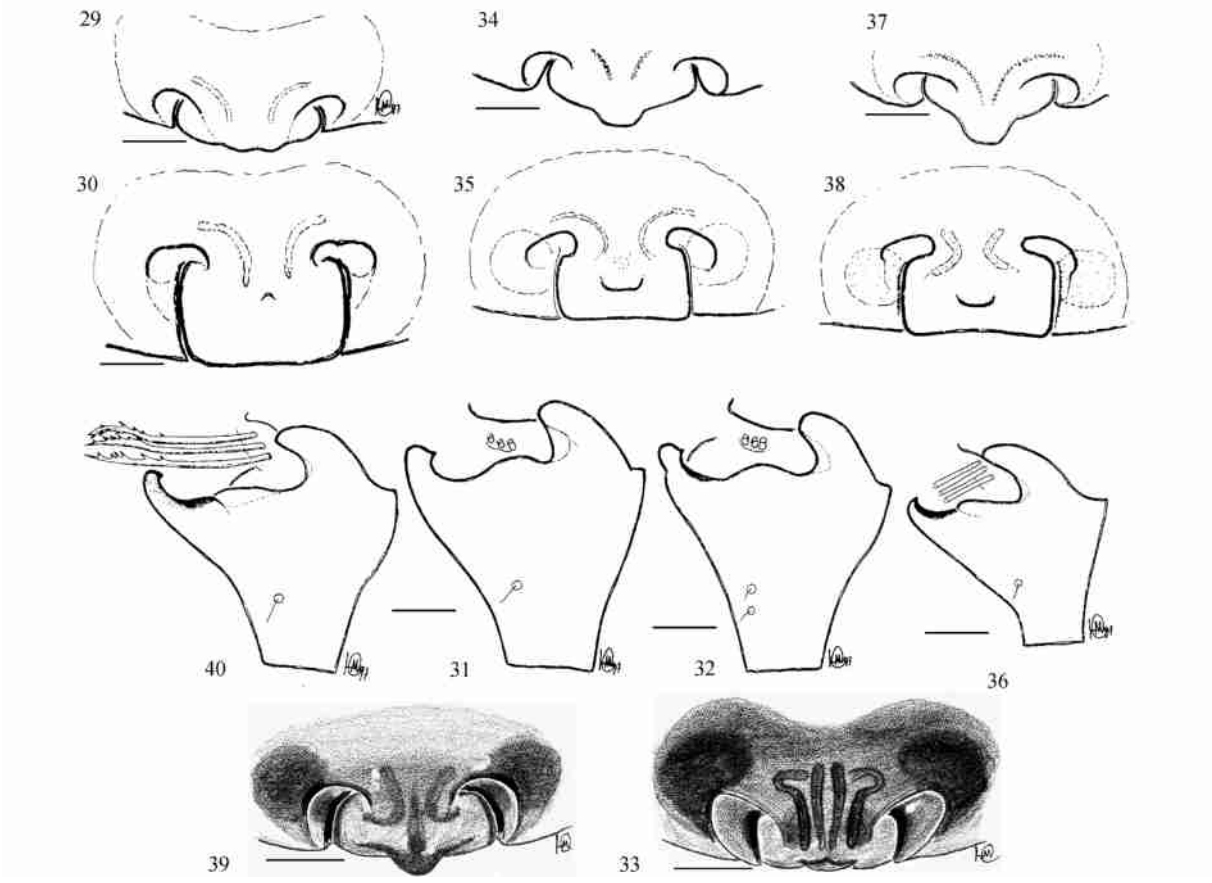
1.65–1.93/1.43–1.6 long, 1.2–1.4/1.1–1.17 wide. Carapace length/tibia I length ratio: 1.22–1.26/1.3–1.36. Tm I 0.75/0.74, Tm IV 0.81/0.78. Specimens from Kevo, northern Finland are about the same in size: Total length: 2.9–4.0/3.6–4.1. Carapace: 1.6–1.86/1.5–1.55 long, 1.21–1.34/1.2–1.3 wide. Male carapace with poorly developed submarginal ridge (*Cr*) visible well on SEM figures only (Fig. 1). Frontal cheliceral tooth (*Ft*) in male with steep dorsal slope (Figs. 1–2). Palp as in Figs. 13–18, 28, 36, 45–46, 68–69. Retrolateral tibial apophysis with a deep but short hollow (*Th*). Epigyne as in Figs. 34–35, 47, 55–57, 70–72, with relatively short rostrum, which is not clearly separated from the median plate. Terminal part of epigynal sulci directed medially and slightly up (Figs. 35, 57).

Diagnosis. *Z. altrigera* is very similar to *Z. orientalis* sp. nov. Females of the two species can be separated by the shorter epigynal rostrum in *Z. altrigera*, and by the posterior part of the outer margins of the epigynal sulci (*Se*) which are sharply in-turned in *Z. cultrigera* (Fig. 57) but nearly straight and parallel with the margins of the median plate in *Z. orientalis* sp. nov. (Fig. 60). The median (*Mp*) and lateral plates (*Lp*) of the epigyne meet at the bottom of the sulci 1/3 the way from its outer edge in *Z. altrigera* (Fig. 55) but at approximately midpoint in *Z. orientalis* sp. nov. (Fig. 58), giving width ratios (*Wr*) of 1: 2 in the former species and 1: 1 in the latter. Males of *Z. altrigera* have relatively shorter lateral tibial apophysis with a deeper and shorter hollow. *Z. cultrigera* can be easily distinguished from the Nearctic species by the shape of the lateral tibial apophysis, the abruptly sloping dorsal side of the frontal tooth, size of rostrum and shape of the epigynal sulci.

Comments. The three species synonymised with *Z. altrigera* are from Lapland. Comparison of specimens from Yenisei and Lapland reveals no differences, and we therefore confirm the synonymy of these species.

Habitats. This species is common in northern Finland where it occurs in varied habitats, both moist and dry, and even in the alpine zone (Palmgren, 1965; Koponen, 1977). In Southern Finland, where it is less abundant, *Z. altrigera* lives chiefly in moss (e. g. *Hyloconium*) in spruce forests (Palmgren, 1976). In Middle Siberia *Z. altrigera* has been found in primary pine-spruce forest, in riverside spruce forest with green mosses, in flood-plane meadows, valley willow and alder stands and in *Carex* bogs (Eskov, 1988).

Distribution. Although *Z. altrigera* has been considered a Holarctic species (cf. Platnick, 2006) it is



Figs 29–40. Epigyne and male palp of *Zornella armata* (29–30, 32–33. Alaska. 31. NWT), *Z. altrigera* (34–36. Kevo. Lapland) and *Z. orientalis* sp. nov. (37–40. Magadan). 29, 33–34, 37, 39. Epigyne, dorsal. 30, 35, 38. Epigyne, caudal. 31–32, 36, 40. Palpal tibia, dorsal. Scale bars = 0.1 mm.

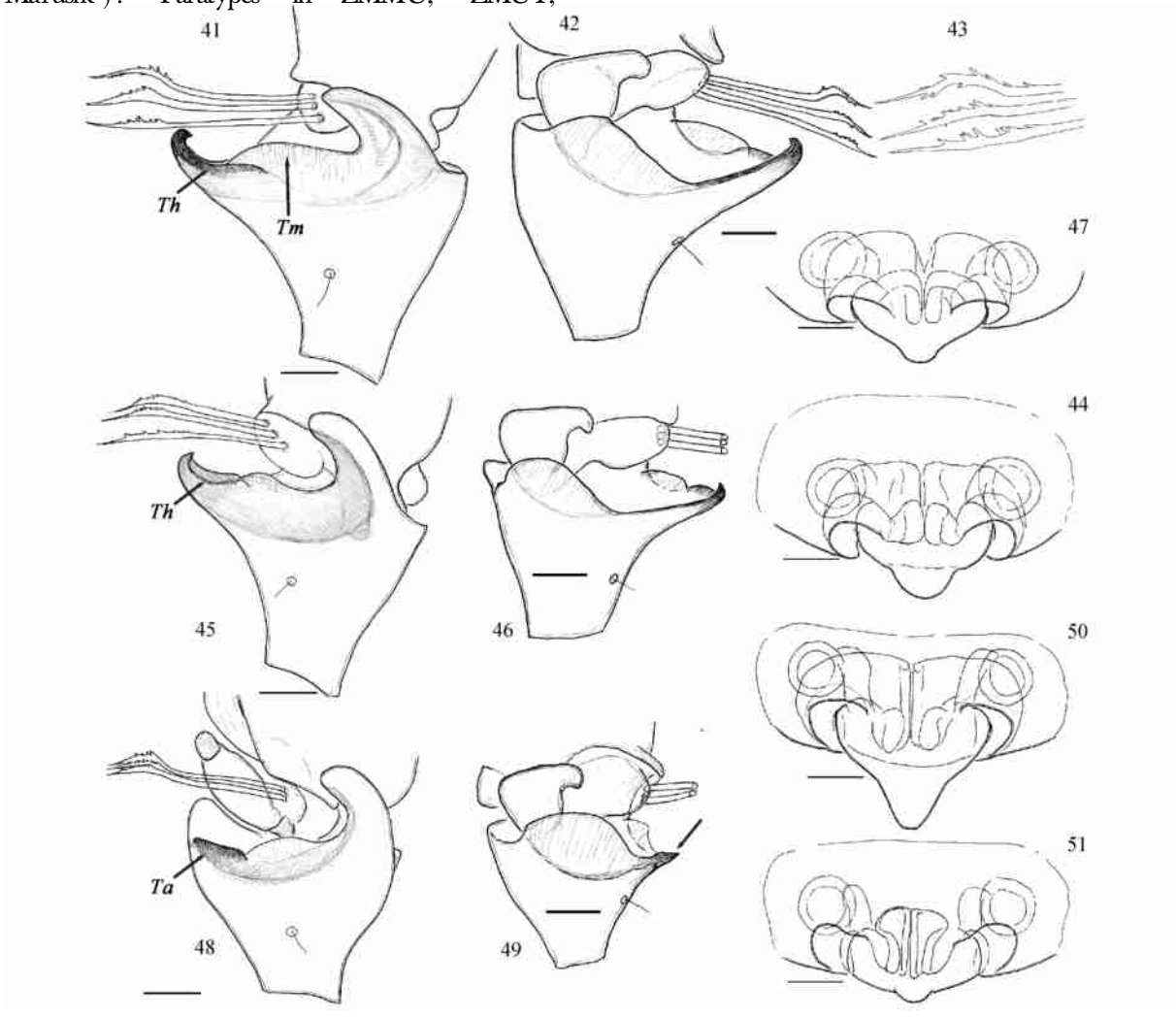
actually restricted to Palaearctic, ranging from Norway and Poland to Yakutia and south to the East-Kazakhstan Area and northern Mongolia (Fig. 79). The northernmost records lie in Northern Norway (70°10′N) and Norilʹsk (69.5°N). In Northeastern Siberia it is replaced with the sibling *Z. orientalis* sp. nov. All Nearctic records of this species are misidentifications of *Z. armata* or *Z. cryptodon*.

Zornella orientalis **sp. nov.** (Figs. 7, 26, 37-44, 58-60, 73-76)

Z. cultrigera: Marusik *et al.*, 1992: 148; Marusik, 1993: 217.
Z. cf. *cultrigera*: Marusik, 2005a: 201; Marusik, 2005b: 279.

Etymology. The specific name reflects eastern distribution of this taxon in Eurasia.

Material examined. Russia: Magadan Area: holotype ♂, together with 3 ♂♂, 6♀♀ (ZMMU), 29 km N of Magadan, Dukcha River Valley near Snow Valley Vill., 59°43′N, 151°E, 12-14 Sep. 1986 (Yu. M. Marusik). Paratypes in ZMMU, ZMUT, MMUM, CNC: 17♀♀, 15 km E of Magadan, Gertner Bay, 27 Sep. 1996 (Yu. M. Marusik); ♂♂♀♀, 29 km N of Magadan, Dukcha River Valley, 59°43′N, 151°E, Summers, 1999-2000 (S. P. Bukhkalo & Bragina); 1 ♂, 5♀♀, 29 km N of Magadan, Snow Valley Vill., Dukcha River Valley, 59°44′N, 151°E, 12-26 Sep. 1995 (Yu. M. Marusik); 2 ♂♂, 2♀♀, 29 km N of Magadan, Snow Valley Vill., Dukcha River Valley, 59°44′N, 151°E, 12-29 Sep. 1996 (Yu. M. Marusik); 4♀♀, Magadan, Marchekan Mt., 17 Sep. 1994 (Yu. M. Marusik); 1 ♂, 1♀ 1juv., Magadan, Marchekan Mt., 59°31′N, 150°49′E, 5 Aug. 2002 (Yu. M. Marusik); 2♀♀, NE Siberia, environs of Magadan, Sep. 2002 (Yu. M. Marusik); 2 ♂♂, Magadan, Marchekan Mt., N macroslope, 3 May 1994 (A. S. Ryabukhin); 8 ♂♀, E vicinities of Magadan, p/t, 25 June-4 Sep. 2001 (K. Starenchenko); 2♀♀, Koni Peninsula, Khindzha River middle flow, 200 m, 11-24 June 1988 (S.



Figs 41-51. Epigyne and male palp of *Zornella orientalis* sp. nov. (41-44. Magadan), *Z. cultrigera* (45-47. Mirnoye), *Z. cryptodon* (48-50) and *Z. armata* (51. NWT). 41, 45, 48. Palpal tibia, dorsal. 42, 46, 49. Palpal tibia, retrolateral. 43. Terminal part of serrated macrosetae. 44, 47, 50-51. Macerated epigyne, ventral. Scale bars= 0.1 mm. Abbreviations: *Ta*- retrolateral tibial apophysis; *Th*- hollow of *Ta*; *Tm*- membrane of tibia; *Tr*- trichobothrium.

Pleshchenko); ♀♀, ca 20 km E of Magadan, Chosenia forest near Ola River bridge, 59°36′N, 151°18′E, 8-21 July 1997 (S. Koponen); 1♀, 137th km of Kolyma Hwy., 60°25′N, 151°30′E, Ola River, valley forest, 28 Sep. 1994 (Yu. M. Marusik); 4♂♂, 6♀♀, upper reaches of the Kolyma River (ca. 62°N), Sibit-Tyellakh River basin, Olen's Creek, foothills of Bol'shoy Annychag Mt. Range, "Aborigen" Field Station, Summer 1986 (Yu. M. Marusik).

Description. Measurements (♂/♀, Snow Valley). Total length: 3.7-4.25/3.25-4.25. Carapace: 1.85-2.21/1.54-1.71 long, 1.36-1.5/1.16-1.24 wide. Carapace length/tibia length ratio: 1.27-1.41/1.22-1.37. Tm I 0.72-0.80/0.75. Tm IV 0.79/0.71. Submarginal ridge on male carapace present but indistinct. Frontal cheliceral tooth with steep dorsal side (Fig. 7). Palp as in Figs. 26, 40-43, 73-74. Retrolateral apophysis (*Ta*) is rather long and has a long, shallow hollow (*Th*). Epigyne as in Figs. 37-39, 44, 58-60, 75-76, with relatively long rostrum, which is more or less clearly separated from the median plate by the lateral concavities. Epigynal sulci long, their terminal parts almost parallel (Figs. 38, 60).

Diagnosis. *Z. orientalis* sp. nov. is very similar to *Z. altrigera*. Females of the two species can be separated by the longer epigynal rostrum in *Z. orientalis* sp. nov., and by the outer margins of the epigynal sulci (*Se*) which are parallel in *Z. orientalis* sp. nov. (Fig. 60) but in-turned in *Z. altrigera* (Fig. 57). The median (*Mp*) and lateral plates (*Lp*) of the epigyne meet in the bottom of the sulci at approximately the midpoint in *Z. orientalis* sp. n. (Fig. 58), but 1/3 the way from the outer edge in *Z. altrigera* (Fig. 55). Males of *Z. orientalis* sp. nov. have longer lateral apophysis with a less shallow hollow. The new species can be easily separated from its Nearctic congeners by the shape of epigynal rostrum, steep dorsal slope of the frontal tooth, and long retrolateral tibial apophysis which has a distinct hollow.

Habitats. In the upper reaches of the Kolyma River it occurs only in the forest belt where it has been found, infrequently, in birch and alder stands. In coastal areas it is relatively common in birch and alder stands with herbs beneath.

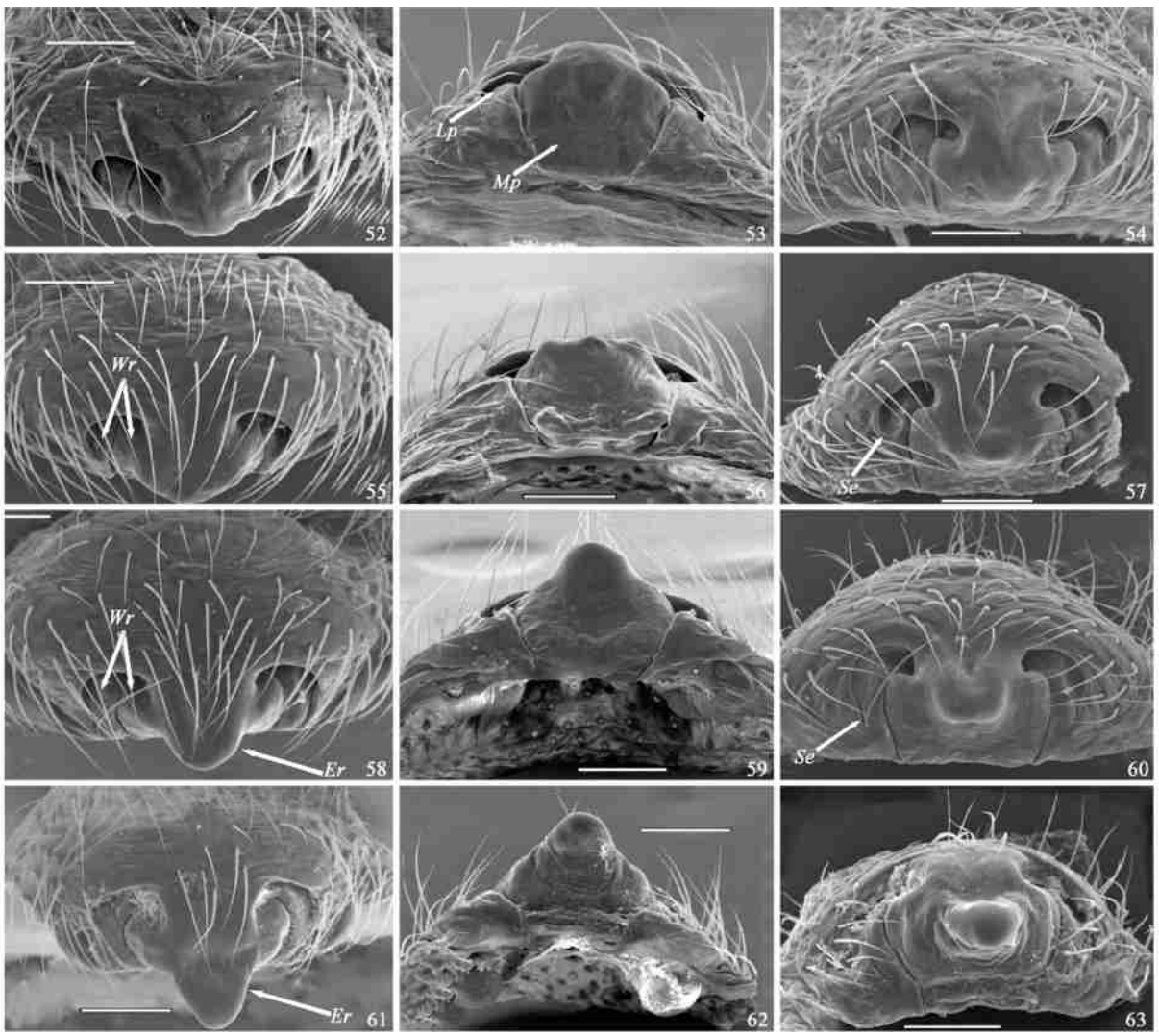
Distribution. *Z. orientalis* sp. nov. appears to be restricted to Northeastern Siberia where it occurs in northern Cisokhotia and along the upper reaches of the Kolyma River (Map 1).

Zornella armata **(Banks, 1906)** (Figs. 8-9, 21-25, 29-33, 51-54, 64-67)

Tmetias armatus Banks, 1906: 98, pl. 2, f. 12 (D ♂).
Lophocarenum armatum: Emerton, 1911: 393, pl. 2, f. 8 (♂D♀).
Gongylidium armatum: Emerton, 1920: 315.
Tmetias altrigerus: Crosby & Bishop, 1928: 1052.
Z. altrigera: Crosby & Bishop, 1933 (in part): 162, pl. 9, f. 214-215 (♂♀).
Z. altrigera: Paquin & Dupérré, 2003: 129, f. 1396-1398 (♂♀).

Material examined. USA: Alaska, 2♂♂ (AMNH, det. Å. Holm as *Z. altrigera*), Anchorage, 8 Aug. 1948 (R. I. Sailer); 1♂, Primrose Camp, 18 km N of Seward, 60°20′N, 149°20′W, 24 Aug. 1968 (W. Ivie). Vermont: 8♂♂ (CNC), Mount Mansfield, 26 May-15 June 1982 (C. D. Dondale & J. H. Redner). Canada: *Yukon Territory*: 2♂♂ (CNC), Carcross, sand dune, June 1981-3 July 1981 (C. D. Dondale); 2♀♀, Kluane Lake, Cultus Bay, 61°11′N, 138°20′W, h 4 000 f, willows in small depression with *Aulacomium* and Hypnum mosses, 13 July 1993 (Yu. M. Marusik); 1♀ Kluane Lake, Cultus Bay, 61°11′N, 138°20′W, h 4 000 f, willow grove with Graminacea on the N slope near ridge, 13 July 1993 (Yu. M. Marusik); 1♀, Kluane Lake, Cultus Bay, 61°11′N, 138°20′W, Rat Lake, willow groves with *Equisetum* and *Carex* on the swampy bank, 23 July 1993 (Yu. M. Marusik); 1♀, Kluane Lake, Cultus Bay, 61°11′N, 138°20′W, small lake on moraine, north steep bank with mosses, under stones and dead tree branches, 21 July 1993 (Yu. M. Marusik); 1♂, Kluane Lake, Christmas Bay, 61°03′N, 138°21′W, willows, 22 July 1993 (Yu. M. Marusik); 1♀ (CNC), North Fork Pass, Demster Hwy., in shrubs, 22 June 1981-03 July 1981, C. Dondale; 1♂, 1♀ (AMNH, det. W. Ivie as *Z. altrigera*), Whitehorse, 60°35′N, 134°59′W, 22 Aug. 1949 (W. Ivie); 1♀ (DJB), Whitehorse, 11 Aug. 1987-16 Aug. 1987 (R. G. Holmberg). Northwest Territories: 1♀ (DJB), Fort Laird, 8 June 1974-22 June 1974 (Wayne Harris); 1♀ (CNC) 2 mi SE Fort Simpson, 15 June 1972-20 June 1972 (A. Smetana), 1♀ (CNC), Inuvik, 11 July 1980-14 July 1980 (L. Humble); 1♀ (CNC), Norman Wells, 1 May 1953 (C. D. Bird); 14♂♀ (AMNH, det. W. Ivie as *Z. altrigera*), Stagg River Camp, 62.46°N, 115.45°W, 12 Aug. 1965 (J. & W. Ivie); 2♀♀ (CNC, 2 vials), Wrigley, 1 June 1969-12 June 1969 (G. E. Shewell); British Columbia: 2♀♀ (DJB), Laird River, 8 Aug. 1987-18 Aug. 1987 (R. G. Holmberg); 1♀ (CNC), 17.5 km S Sikianni River, Alaska Hwy., 31 May 1981-8 July 1981 (C. D. Dondale); 1♀ (CNC), Summit Lake, mile 392, Alaska Hwy., 15 June 1959 (R. E. Leech); 5♀♀ (CNC) Testa River, mile 378, Alaska Hwy., spruce-poplar forest, 31 May 1981-8 July 1981 (C. D. Dondale); Alberta: 1♀ (DJB), Athabasca, white spruce heath, 2 July 1986-16 July 1986 (R. G. Holmberg); 1♀ (AMNH, *Tmetias armatus* B.), Banff, April, Under snow; 31%, 6♀♀ (DJB, 12 vials), Baptiste Lake, 1987-1988 (R. G. Holmberg); 14♀♀ (UASM) Birch Mountains Wildland Park, Gardiner Lake, open black spruce, 15 June 2004-9 July 2004 (Ted Johnson); 19♀♀ (UASM, 7 vials), Caribou Mountains Wildland Park, Wentzel Lake, July 2003 (Ted Johnson, G. J. Hiltchie); 1♀ (CNC), Cypress

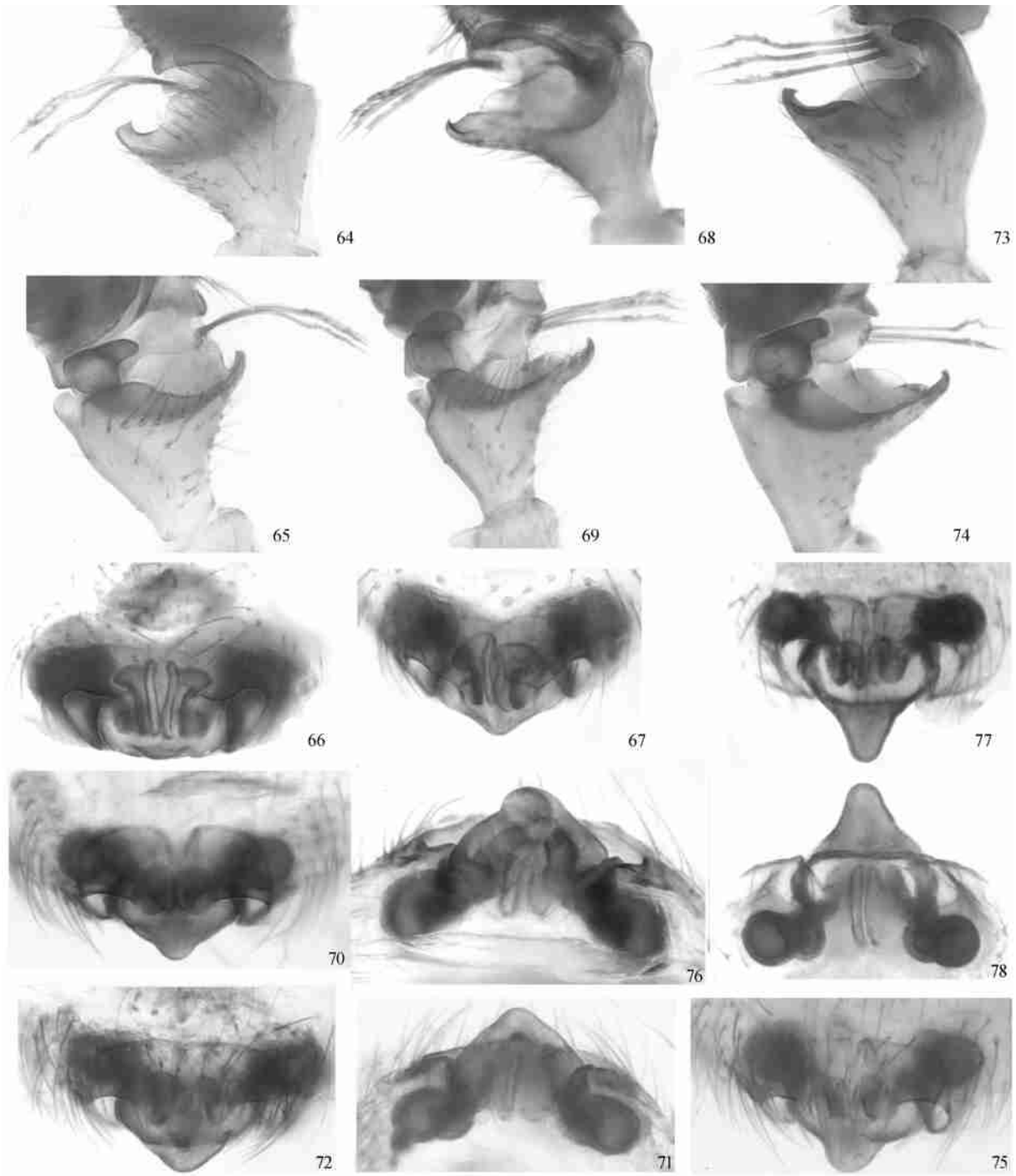
Hills Provincial Park, pine woods, 8 June 1973-15 June 1973 (J. D. Redner & C. Starr); 1♀ (UASM), 20 km NW Dixonville, 22 June 1999 (D. Shorthouse); 24 ♂♂, 30♀♀ (DJB, 14 vials), Edmonton, spruce woods, 1982-1983 (R. G. Holmberg); 1♀ (DJB), 10 km SE Exshaw, 29 June 1987-6 July 1987 (R. G. Holmberg); 1♀ (DJB), Mariana Lake, 10 Aug. 1987-20 Aug. 1987 (R. G. Holmberg); 5 ♂♂, 26♀♀ (DJB, 10 vials), 25 km SW Rocky Mt. House, pine forest, 1994-1995 (H. Carcamo); 1 ((DJB), 10 mi S Seebe, 10 July 1985-15 July 1985 (R. G. Holmberg); 1♀ (DJB), 11 km N Slave Lake, 27 June 1996 (Hammond); 1 ♂ (DJB) 11 km S Slave Lake, 24 Sep. 1996 (Hammond); 2 ♂♂ (CNC), Sulfur Mountain, Banff, 1916; 2 ♂♂ (DJB), 10 km N Wandering River, 10 Sep. 1987-18 Sep. 1987 (R. G. Holmberg. Saskatchewan: 1 ♂ (DJB), Anglin Lake, 53° 44′ N, 105° 56′ W, moss in spruce/aspen forest, 26 Aug. 1993-29 Aug. 1993 (D. J. Buckle); 2 ♂♂, 1♀ (DJB), Anglin Lake, 55° 25′ N, 106° 00′ W, basin fen & surrounding, Picea mariana woods, 28 Oct. 1995-21 May 1996 (D. J. Buckle); 2♀♀ (DJB), Besnard Lake, 1 June 1970 (D. J. Buckle); 1 ♂, 3♀♀ (DJB), Besnard Lake, mixed woods, 1 Sep. 1972-6 Sep. 1972 (D. J. Buckle). Manitoba: 4♀♀ (CNC, 4 vials), South Indian Lake, 1977 (Michael Collins). Ontario: 2♀♀ (CNC) Lake Superior Provincial Park, Cape Garantua, 7 June 1973 (J. M. Campbell, R. Perry); 1♀ (CNC), Thunder Bay District, 6 mi E Terrace Bay on Route 17, 20 June 1971 (ROM Field Party); 1♀ (CNC), Wawa, mixed forest, 19♀♀, 1961; 1♀ (CNC), Wawa, birch, 18 June 1972. Québec: 7 ♂♂ (ZMUT, det. S. Koponen as *Z. altrigera*), Saguenay, Winter 1992 (R. Gauthier). New Brunswick: 10 ♂♂, 11♀♀ (CNC, 7 vials), Green River 30 mi N Edmonston, 1962-1969 (T. R.



Figs 52-63. Epigyne of *Zornella armata* (52-54, NWT), *Z. altrigera* (55, 57. Mirnoye. 56. Chambe), *Z. orientalis* sp. nov. (58-60. Magadan) and *Z. cryptodon* (61-63). 52, 55, 58, 61. Ventral. 53, 56, 59, 62. Caudal. 54, 57, 60, 63. Ventro-caudal. Scale bars= 0.1 mm. Abbreviations: *Er*- epigynal rostrum; *Lp*- lateral plate; *Mp*- median plate; *Se*- terminal part of epigynal sulci; *Wr*- width ratio.

Renault); Nova Scotia: 2♀♀ (CNC), Cape Breton Highlands National Park, North Mountain, 11 July 1983–19 July 1983 (L. Masner); 1♀ (CNC), Cape Breton Highlands National Park, North Mountain, 25 June 1983 (Y. Bousquet); 2♀♀ (CNC), Cape Breton Highlands National Park, Paquette Lake, 29 July 1983 (D. E. & J. E. Bright).

There are literature records from White Mountain near Crawford Notch, NH (Emerton, 1911), Presque Isle, ME, and Mount Whiteface, Mount Marcy and Hague, NY (Crosby & Bishop, 1933), Gaff Topsail Mountain, NF (Hackman, 1954), Mont du Lac des Cygnes and Forillon National Park, QC (Bélanger & Hutchinson, 1992), and Parc de Conservation de la Gaspésie, Québec (Paquin & LeSage, 2000). Pierre Paquin (pers. com., 2006) reports the presence of this



Figs 64–78. Male palp and epigyne of *Zornella armata* (64–65, 67. NWT; 66. Yukon T.), *Z. altrigera* (68–70. Mirnoye. 71–72. Kevo), *Z. orientalis* sp. nov. (73–76. Magadan) and *Z. cryptodon* (77–78). 64, 68, 73. Palpal tibia, dorsal. 65, 69, 74. Palpal tibia, prolateral. 66–67, 70, 72, 75, 77. Macerated epigyne, ventral. 71, 76, 78. Macerated epigyne, caudal.

species at Abitibi, Québec.

Description. Measurements (♂/♀, Stagg River). Total length 4.0-4.6/3.5-3.75. Carapace: 2.03-2.14/1.5-1.6 long, 1.5-1.53/1.2-1.3 wide. Carapace length/tibia Ⅰ lengthratio: 1.2-1.23/1.3. Tm Ⅰ 0.81/0.79, Tm Ⅳ 0.79/0.82. Male has distinct submarginal ridge along lateral side of thorax (*Cr*, Fig. 1). Frontal tooth of chelicera usually with denticle on dorsal side (Figs. 8-9). Mastidion often distinctly bifid. Palp as in Figs. 21-25, 31-32, 64-65. Retrolateral tibial apophysis with distinct lateral protuberance (Figs. 22, 64), shape of this apophysis is very sensitive to the angle of observation. Epigyne as in Figs. 29-30, 33, 51-54, 66-67. Rostrum is almost undeveloped.

Diagnosis. Males of this species can be easily separated from all congeners by the finger-like retrolateral tibial apophysis with a small lateral protuberance (Fig. 64), and by the distinct submarginal ridges on the carapace, lacking in other species. Additionally, the cheliceral frontal tooth of the male frequently has a dorsal knob, which other species lack (Figs. 8-9). Females are distinguished by the lack of a distinct epigynal rostrum (Fig. 66).

Habitats. It has been collected from surface litter and moss in both deciduous and conifer forest throughout the boreal zone.

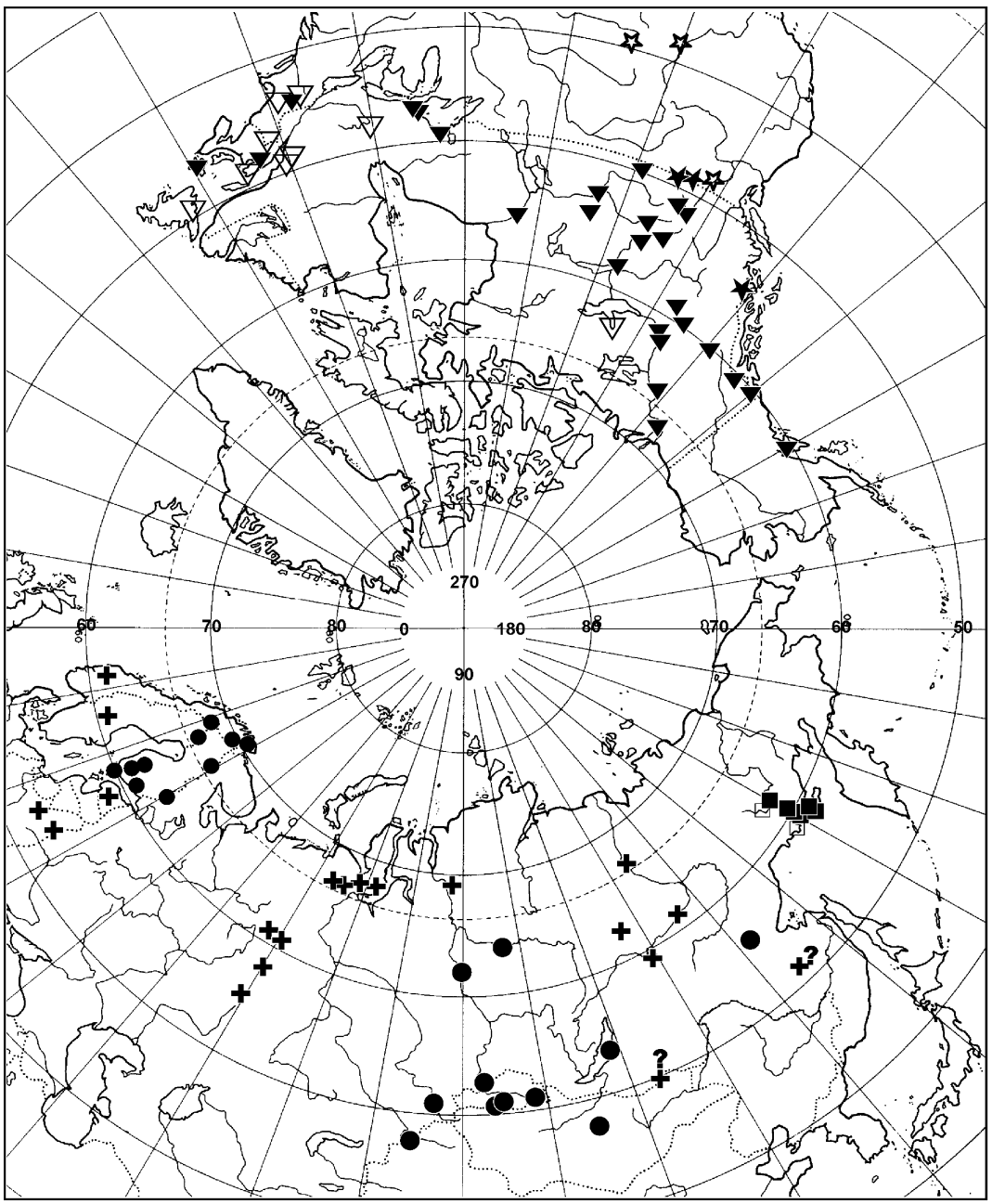


Fig. 79. Distribution of *Zomdla* species: *Z. altrigera* (● & ┼), *Z. orientalis* sp. nov. (■), *Z. armata* (▲) and *Z. cryptodm* (★). Cross and open figures refer to literature or state records.

Distribution. The type locality of *Zornella armata* is "Manitoba". This species is found in the mountains of northern New England and throughout the boreal forest region from the maritime provinces of Canada west to northern British Columbia and Alaska. A disjunct population occurs in the Cypress Hills of southeastern Alberta, an isolated outlier of the Rocky Mountain foothills in the midst of the Great Plains (Map 1). The Cypress Hills flora and fauna have mixed boreal and western montane affinities.

Zornella cryptodon **(Chamberlin, 1920)** (Figs. 10-12, 19-20, 27, 48-50, 61-63, 77-78)

Diplocephalus cryptodon Chamberlin, 1920: 196, f. 21.1-3 (D ♂♀).
Zornella caltrigera: Crosby & Bishop, 1933 (in part): 162.
Hybauchenidium sp. # 1: Crawford, 1988: 18.

Material examined. Canada: *British Columbia*: 1♀ (RGB) Copper River Valley near Terrace, 6 July 1995-26 July 1995 (J. Lemieux). Alberta: 1 ♂ (DJB), Blood Indian Reservation 148A, 49°03′ N, 113°42′ W, burned lodgepole pine/aspen forest, 5200′ (E. Kinsella); 1♀ (DJB), Chinook Lake, 49°40′ N, 14°30′ W, 4800′, open spruce/fir woods, 26 July 1988 (D. J. Buckle); 41♀♀ (DJB), Waterton Lakes National Park, 49°04′ N, 113°47′ W, lodgepole pine/aspen forest, 5200′, 26 June 2000-3 July 2000 (E. Kinsella); 9♀♀ (DJB), Waterton Lakes National Park, 49°04′ N, 113°47′ W, lodgepole pine/aspen forest, 5200′, 31 July 2000-7 Aug. 2000 (E. Kinsella); 51 ♂♂, 66♀♀ (DJB, 5 vials), Waterton Lakes National Park, 49°04′ N, 113°47′ W, lodgepole pine/aspen forest, 5200′, 28 Aug. 2000-11 Sep. 2000 (E. Kinsella); 1♀ (CNC), Waterton Lakes National Park, Cameron Lake, under shrubs, edge of seepage meadow, 17 June 1980-28 June 1980 (I. M. Smith); 1♀ (CNC), Waterton Lakes National Park, Cameron Lake, 5300′, 19 June 1980-28 June 1980 (J. M. Campbell); 1♀ (CNC), Waterton Lakes National Park, Cameron Lake, 5300′-5500′, 9 June 1980-19 June 1980 (J. M. Campbell); 1♀ (CNC), Waterton Lakes National Park, edge of meadow near mixed coniferous woods, 12 June 1980-16 June 1980 (I. M. Smith); 1♀ (CNC), Waterton Lakes National Park, edge of meadow near mixed coniferous woods, 17 June 1980-28 June 1980 (I. M. Smith); Waterton Lakes Natl. Park, Lookout Butte, 9 June 1980 (J. M. Campbell); 1♀ (CNC), Waterton Lakes National Park, mile 6, Chief Mountain Hwy., 4500′, 14 June 1980-28 June 1980 (J. M. Campbell).

Literature records include the "Utah" type locality (Chamberlin, 1920) and a female from 48.9°N, 117°W in the northeastern corner of Washington state (Crawford, 1988). Identification of the Washington specimen was confirmed from drawings provided by Rod Crawford. Joey Slowik (pers. com., 2006) reported the presence of 1 ♂ in the Denver Museum of Nature & Science collection (Colorado: Clear Creek Co.: Squaw Mountain, 39°40′05″N, 105°31′33″W, 10800 feet, pit trap, 3 Sep. 2005-4 Oct. 2005, J. Slowik). Its identity was confirmed by comparison of the specimen with illustrations for this paper. The "Montana" and "Vancouver Island" records in Emerton (1920) may apply to this species but examination of the specimens will be necessary to confirm this.

Description. Measurements (♂/♀). Total length 3.0-3.4/3.0-3.13. Carapace: 1.4-1.45/1.36-1.43 long, 1.1-1.15/1.0-1.07 wide. Carapace length/tibia I lengthratio: 1.38-1.4/1.46. TmI 0.63/0.69, TmIV 0.77/0.76. Frontal tooth with a gradual dorsal slope (Figs. 10-12). Male palp as in Figs. 19-20, 27, 48-49. Retrolateral tibial apophysis reduced to a convex lobe (Figs. 20, 48), its inner side with several ridges (Fig. 19). Female epigyne as in Figs. 50, 61-63, 77-78, with very long rostrum.

Diagnosis. This species can be easily separated from all congeners by its retrolateral tibial apophysis which is reduced to a convex lobe. Females have a very long epigynal rostrum. This species has the lowest TmI ratio (0.63-0.69).

Habitats. It has been collected from forest habitats.

Distribution. The type locality of *Z. cryptodon* is "Utah". It is a western North American species, found from central British Columbia and southwestern Alberta south to Utah and Colorado (cf map).

Acknowledgements We wish to thank Vladimir I. Ovtsharenko for help in arranging a trip for the senior author to New York in 1997, Norman I. Platnick for providing comparative material, Michael I. Saaristo for valuable comments on relationships of *Zornella*, and Veikko Rinne (Turku) for help in practical work. Charles Dondale (CNC), Kirill G. Mikhailov (ZMMU), Darrell Ubick (CAS), and Robb Bennett kindly loaned material from their collections. Rod Crawford (Burke Museum) and Joey Slowik (DMNS) provided information on material in their collections, and Torbjorn Kronestedt (Naturhistoriska riksmuseet) translated parts of Holm (1963) relating to *Zornella*. This work was supported in part by the Russian Foundation for Basic Research (grant 04-04-48727) and INTAS grant (05-1000008-8224).

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